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# Two new species of the loach genus *Homatula* Nichols, 1925 (Pisces, Nemacheilidae) from the upper Chang-Jiang Basin in China

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## Abstract

Two new species of *Homatula* are herein described from the Wu-Jiang of the upper Chang-Jiang Basin in Guizhou Province, China. *Homatula xiangzhi* and *H. shexiang* are respectively assigned to the scaleless group and the partially scaled group of the genus. *Homatula xiangzhi* differs from all other species of the scaleless group in having a complete lateral line, an adipose crest along the dorsal mid-line of the caudal peduncle anteriorly terminating behind the middle of the anal-fin base, nine branched dorsal-fin rays, vertebrae 4+42-43 and no median notch on the lower jaw. *Homatula shexiang* is similar to *H. longidorsalis* in having nine branched dorsal-fin rays rather than seven or eight in all other species of the partially scaled group, but differs from it in having an adipose crest along the dorsal mid-line of the caudal peduncle anteriorly terminating behind the middle of the anal-fin base, a deeper head and a slender caudal peduncle. The validity of the two new species is further corroborated in a molecular phylogenetic analysis, based on the Cytb gene.

## Key Words

Cypriniformes, molecular phylogeny, morphology, taxonomy, Wu-Jiang

## Introduction

Within the family Nemacheilidae, the genus *Homatula* is characterised by possessing adipose crests along dorsal and ventral mid-lines of the caudal peduncle (Nichols and Pope 1925; Hu and Zhang 2010; Min et al. 2022). Currently, it comprises 28 species from southern China and central Vietnam (Li et al. 2022; Che et al. 2023). This genus has a concentrated distribution in the upper Chang-Jiang Basin where six species have been documented: *H. berezowskii* (Günther, 1896), *H. oxygnathra* (Regan,1908), *H. potanini* (Günther, 1896), *H. tigris* Che, Dao, Chen, Pan, Hua, Liang & Wang, 2023, *H. variegata* (Sauvage & Dabry de Thiersant, 1874) and *H. wujiangensis* (Ding & Deng, 1990) (Guo et al. 2021; Liu et al. 2022; Che et al. 2023). Amongst them, three species, misplaced in *Nemacheilus* or *Paracobitis*, were previously reported from the Wu-Jiang, the largest tributary on the southern bank of the upper Chang-Jiang mainstream: *H. potanini*, *H. variegata* and *H. wujiangensis* (Wu 1989; Ding 1994; Yang et al. 2022). However, their identification needs re-evaluation especially given the taxonomic revisions of some relevant congeneric species outside this river during the past decade or more. For example, *H. variegata*, previously recognised as a species widespread in the upper Zhu-Jiang (Nanpan-Jiang), the upper Chang-Jiang and Huang-He Basins (Zheng 1989; Zhu 1989; Yang et al. 1994; Guo et al. 2021), was the taxonomic subject of many works (Hu and Zhang 2010; Gu and Zhang 2012). It is widely thought that its type locality was in the upper Chang-Jiang Basin. Kottelat (2012), though, asserted that the type locality of *H. variegata* was

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in the Huang-He Basin. This hypothesis has been recently corroborated on the basis of examination on the type and topotypical specimens (Liu et al. 2022); *H. variegata* is truly represented by the population of the Wei-He, a tributary of the middle Huang-He Basin (Liu et al. 2022). In this context, it is urgently needed to assess the taxonomic status of specimens under the name of *H. variegata* from the Wu-Jiang or even from the upper Chang-Jiang Basin.

Field survey of fishes, conducted by us into the Wu-Jiang, yielded many specimens referred to as *H. variegata*, following the identification of this species by Zheng (1989), Wu (1989) and Ding and Deng (1990). These specimens were scrutinised to represent two undescribed species under a reliable taxonomic framework integrating morphological and molecular evidence. The purport of the present study is to provide a formal description of the two undescribed species, here named as *H. xiangzhi* sp. nov. and *H. shexiang* sp. nov., respectively.

## Materials and methods

Fishes, utilised for this study, were collected in accordance with the Chinese Laboratory Animal Welfare and Ethics animal welfare laws. Specimens were captured during fish surveys conducted in 2018 and 2020. After being anaesthetised, all caught individuals were killed by immersion in ethanol or formalin. Captured specimens were either stored in 95% ethanol for DNA extraction or initially fixed in 10% formalin and then transferred to 70% ethanol for morphological examination.

All morphometric measurements and meristic counts were made on the left side of each individual when possible, following the methods utilised by Kottelat (1990). Measurements were taken point to point with digital calipers directly linked to a data-recording computer and data recorded to the nearest 0.1 mm. Meristic counts were made utilising a bilocular Zeiss Stereo Discovery V6; the last two branched rays in dorsal and anal fins, closely approximated at the base, were counted as a single ray. Micro-CT imagines were used to observe skeletal structures including the count of vertebrae. The Weberian apparatus was regarded as including four vertebrae. All meristic counts and morphometric measurements were provided in Table 2.

Genomic DNA was extracted from alcohol-preserved fin clips using the TIANamp Genomic DNA Kit (Tiangen Biotech, Beijing). Mitochondrial Cytb gene was amplified using polymerase chain reaction (PCR) with primers L14724 (GACTTGAAAAACCA CCGTTG) and H15915 (CTCCGATCTCCGGATTACAAGAC) (Xiao et al. 2001). The following thermal cycling profiles were adopted: 95 °C pre-denaturing (5 min), 94 °C denaturing (50 s), 53 °C for Cytb annealing (90 s), 72 °C extension (10 min), for 34 cycles, and 72 °C final extension (10 min) and then the product was preserved at 4 °C. Amplified products were subsequently purified and utilised for direct cycle sequencing by the Aoke Dingsheng Sequencing Company.

Twelve samples of *H. xiangzhi* (five) and *H. shexiang* (seven) were amplified for the Cytb gene. Four samples of *H. berezowskii* captured from the Han-Jiang and two samples of *H. wujiangensis* from the Wu-Jiang in our other field surveys were determined for the same gene (Table 1). Sequence data were archived in the public domain database GenBank. These sequences were subject to phylogenetic analysis, along with 46 GenBank- retrieved sequences from 23 congeneric species of *Homatula*. Sequences from two species of *Schistura* (*S. fasciolata* and *S. longa*) and two species of *Triplophysa* (*T. stoliczkai* and *T. stenura*) were used as outgroups (Table 1). Multiple alignments were prepared with MEGA 7.0 software for all sequences (Kumar et al. 2016). The general time-reversible model with invariant sites and a gamma distribution variation across sites (GTR+F+G4) was selected as the best-fitting model for the Cytb gene in ModelFinder (Kalyaanamoorthy et al. 2017), based on Akaike's Information Criterion (Akaike 1974). MrBayes 3.2.6 (Ronquist et al. 2012) was used to calculate Bayesian Inference (BI) tree and IQ-TREE v.1.6.8 (Nguyen et al. 2015) was applied to generate the Maximum-Likelihood (ML) tree. Two independent parallel Markov Chain Monte Carlo runs were monitored with Tracer v.1.7.1 (Rambaut et al. 2018) and the first 25% samples were discarded as burn-in. The tree was rooted by outgroups and visualised via FigTree v.1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/).

All specimens, utilised in this study, are archived in the ichthyological collection at the Institute of Hydrobiology (IHB), Chinese Academy of Sciences, Wuhan City, Hubei Province, China. Photographic examination was made for types of *H. disparizona*, *H. longidorsalis* and *H. nanpanjiangensis* that are so far housed in the Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences, Kunming City, Yunnan Province, as well as *H. oxygnathra* and *H. variegata* which are respectively deposited in the British Museum of Nature and History (BMNH) and the Muséum National d'Histoire naturelle de Paris (MNHN).

## Availability of data and material

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

## Results

### *Homatula xiangzhi* Cao, Liu, Zeng & Zhang, sp. nov.

https://zoobank.org/B49514A4-5753-4411-8156-4C43D6788B8F

Figs 1, 2.

*Nemachelius variegatus*: Wu, 1987: 27 (Nanming-He of Wu-Jiang).

*Paracobitis variegatus*: Ding, 1994: 51 (Wulong County, Wu-Jiang).

**Holotype.** IHB 202006048865, 98.0 mm SL; China: Guizhou Province: Guiyang City: Wudang District: Baishui-He, a tributary of Qingshui-He discharging into Wu-Jiang, at Shanglongjiao Village (26°46'21"N, 106°55'02"E) of Xiangzhi-Gou; collected by Z. X. Zeng in June 2020.

**Table 1.** The detailed information of sequences used in this study with sampling location and GenBank accession number.

| Species | Sampling locality (River basin) | GenBank accession numbers | References |
|---|---|---|---|
| *H. acuticephala* | Eryuan, Yunnan (Lancang-Jiang) | HM010503 | Min et al. (2012) |
| *H. anguillioides* | Eryuan, Yunnan (Lancang-Jiang) | HM010546 | Min et al. (2012) |
| *H. anteridorsalis* | Baoshan, Yunnan | OP779698 | Li et al. (2022) |
| | (Nu-Jiang) | OP779701 | Li et al. (2022) |
| *H. berezowskii* | Shennongjia, Hubei | OM640077 | This study |
| | (Han-Jiang) | PQ816783 | This study |
| | Shiyan, Hubei | PQ816781 | This study |
| | (Han-Jiang) | PQ816782 | This study |
| *H. cryptoclathrata* | Longling, Yunnan | HM010569 | Min et al. (2012) |
| | (Nu-Jiang) | HM010566 | Min et al. (2012) |
| *H. disparizona* | Wenshan, Yunnan | MG238217 | Min et al. (2023) |
| | (Red-River) | MG238218 | Min et al. (2023) |
| *H. geminusclathrata* | Jingdong, Yunnan (Lancang-Jiang) | OP779703 | Li et al. (2022) |
| *H. guanheensis* | Hanzhong, Shaanxi | OL329831 | Liu et al. (2022) |
| | Langao, Shaanxi | OL329833 | Liu et al. (2022) |
| | Xixia, Henan | MT771714 | Zhou et al. (2021) |
| | (Han-Jiang) | MT771715 | Zhou et al. (2021) |
| *H. laxiclathra* | Zhouzhi, Shaanxi | OL329841 | Liu et al. (2022) |
| | Taibai, Shaanxi | OL329846 | Liu et al. (2022) |
| | (Wei-He) | OL329848 | Liu et al. (2022) |
| *H. longibarbata* | Dali, Yunnan | OP779704 | Li et al. (2022) |
| | (Lancang-Jiang) | OP779705 | Li et al. (2022) |
| *H. longidorsalis* | Yiliang, Yunnan | HM010500 | Min et al. (2012) |
| | (Nanpan-Jiang) | HM010568 | Min et al. (2012) |
| *H. microcephala* | Dali, Yunnan | OP779710 | Li et al. (2022) |
| | (Lancang-Jiang) | OP779709 | Li et al. (2022) |
| *H. nanpanjiangensis* | Luoping, Yunnan | HM010574 | Min et al. (2012) |
| | (Nanpan-Jiang) | HM010577 | Min et al. (2012) |
| *H. nigra* | Baoshan, Yunnan | OP779715 | Li et al. (2022) |
| | (Nu-jiang) | OP779716 | Li et al. (2022) |
| *H. oxygnathra* | Yuanmou, Yunnan | OL329836 | Liu et al. (2022) |
| | (Jinsha-Jiang) | OL329835 | Liu et al. (2022) |
| | Yanbian, Sichuan | OL329839 | Liu et al. (2022) |
| | (Yalong-Jiang) | OL329838 | Liu et al. (2022) |
| *H. potanini* | Leshan, Sichuan | JF340385 | Min et al. (2012) |
| | (Jinsha-Jiang) | JF340386 | Min et al. (2012) |
| *H. pycnolepis* | Dali, Yunnan | OP779718 | Li et al. (2022) |
| | (Lancang-Jiang) | OP779719 | Li et al. (2022) |
| *H. shexiang* sp. nov. | Kaiyang, Guizhou | OM640080 | This study |
| | (Wu-Jiang) | PQ816776 | This study |
| | | PQ816775 | This study |
| | | OM640081 | This study |
| | | OM640082 | This study |
| | Xiuwen, Guizhou | OM640083 | This study |
| | (Wu-Jiang) | OM640084 | This study |
| *H. tigris* | Kunming, Yunnan | ON124934 | Che et al. (2023) |
| | (Jinsha-Jiang) | ON124932 | Che et al. (2023) |
| | | ON124933 | Che et al. (2023) |
| *H. variegata* | Xi'an, Shaanxi | OL329850 | Liu et al. (2022) |
| | (Wei-He) | OL329851 | Liu et al. (2021) |
| | Luoning, Henan | OL681884 | Liu et al. (2022) |
| | (Huang-He) | OL681883 | Liu et al. (2022) |
| *H. wenshanensis* | Wenshan, Yunnan (Red-River) | MW548261 | NCBI |
| *H. wujiangensis* | Jinfoshan, Chongqing | PQ816777 | This study |
| | (Wu-Jiang) | PQ816778 | This study |
| *H. wuliangensis* | Pu'Er,Yunnan | HM010517 | Min et al. (2012) |
| | (Lancang-Jiang) | HM010496 | Min et al. (2012) |
| *H. xiangzhi* sp. nov. | Guiyang, Guizhou | OM640088 | This study |
| | (Wu-Jiang) | OM640089 | This study |
| | | OM640090 | This study |
| | | PQ816779 | This study |
| | | PQ816780 | This study |
| *H. dotui* | Vietnam | OK230030 | Nguyen et al. (2021) |
| | | OK230029 | Nguyen et al. (2021) |
| *Schistura fasciolata* | Yunnan, China | KY404236 | NCBI |
| *Schistura longa* | Unknown | JF340408 | Min et al. (2012) |
| *Triplophysa stenura* | Yunnan, China | JN837657 | Min et al. (2012) |
| *Triplophysa stoliczkai* | Unknown | JQ663847 | Li et al. (2013) |

**Figure 1.** *Homatula xiangzhi* sp. nov, IHB 202006048865, holotype, 98.0 mm SL; China: Guizhou Province: Guiyang City: Wudang District: Baishui-He. Lateral (upper), dorsal (middle) and ventral (lower) view.

**Paratypes.** IHB 202006048864, 202006049211–9212, three specimens, 53.7–133.4 mm SL; other date same as holotype. IHB 20180055996–5997, two specimens, 61.0–76.6 mm SL and IHB 202006048866–8867, two specimens, 60.5–73.1 mm SL; China: Guizhou Province: Guiyang City: Wudang District: Pudu-He, a stream tributary to Qingshui-He of Wu-Jiang, at Duzhai Village (26°41'52"N, 113°12'39"E); collected by L. Cao, C. T. An and Z. T. Wang in October 2018 and by D. M. Guo and W. H. Shao in June 2020.

**Diagnosis.** A member of the scaleless group of *Homatula*, defined by having no scales on the body or a small number of scales sparsely scattering over the caudal peduncle. It is distinct from other six species of the group in having a complete (vs. incomplete in *H. wujiangensis*) lateral line, an elongate (vs. stout) body with a uniform depth (vs. non-uniform, gradually decreasing towards the caudal-fin base in *H. wujiangensis* and *H. robusta*), an adipose crest along the dorsal mid-line of the caudal peduncle anteriorly terminating vertically away from the anal-fin origin, but beyond the posterior end of the anal-fin base (vs. above vertical of the posterior end of the anal-fin base in *H. wenshanensis*; above or beyond the anal-fin origin in *H. nanpanjiangensis*, *H. oligolepis*, *H. disparizona* and *H. robusta*), a slender (vs. stout) caudal peduncle with (depth 42.0–53.8% of its length vs. 70.5–78.5% in *H. robusta* and 100.0–120.0% in *H. wujiangensis*) of its length, vertebrae 4+42-43 (vs. 4+47–48 in *H. wenshanensis* and 4+35–41 in remaining species), more branched dorsal-fin rays (9 vs. 7–8 in *H. disparizona*, *H. robusta*, *H. wenshanensis* and *H. wujiangensis*), a truncate (vs. emarginate in *H. disparizona*, *H. nanpanjiangensis* and *H. robusta* and forked in *H. wenshanensis*) and no median notch on the lower jaw (vs. present in *H. nanpanjiangensis*, *H. oligolepis*, *H. robusta*, *H. wenshanensis* and *H. wujiangensis*).

**Description.** Morphometric measurements for type specimens given in Table 2 and general appearance of holotype shown in Fig. 1.

Body elongated, anteriorly cylindrical and posteriorly compressed laterally, with uniform depth from behind head to caudal peduncle. Ventral profile of head straight or slightly concave; ventral profile of body straight or slightly concaved from pectoral-fin insertion to anal-fin origin and slightly convex from anal-fin origin to caudal-fin base. Body nearly scaleless; only a few tiny scales scattered over caudal peduncle. Lateral line complete, with 80–90 pored scales, extending along mid-lateral body to caudal-fin base. Adipose crests along dorsal and ventral mid-lines of caudal peduncle supported by rudimentary rays; dorsal adipose crest anteriorly terminating vertically away from the anal-fin origin, but beyond the posterior end of the anal-fin base and ventral adipose crest anteriorly extending close to posterior end of anal-fin base. Head relatively long and slightly depressed, wider than deep. Snout blunt when viewed laterally, shorter than postorbital head and slightly pointed in dorsal view. Eye oval or elliptical with slightly convex interorbital space, placed

**Figure 2.** Freshly-captured individual of *H. xiangzhi* sp.nov., collected from China: Guizhou Province: Guiyang City: Wudang District: Baishui-He, a tributary of Qingshui-He discharging into Wu-Jiang, at Shanglongjiao Village.

**Table 2.** Morphometric measurements for two new species of *Homatula*.

| Characteristic | *H. xiangzhi* sp.nov. | | | *H. shexiang* sp.nov. | | |
|---|---|---|---|---|---|---|
| | Holotype | Paratypes (n = 7) | | Holotype | Paratypes (n = 15) | |
| | | Range | Mean ± SD | | Range | Mean ± SD |
| Standard length (mm) | 98.0 | 53.7–133.4 | 76 ± 24.8 | 100.2 | 71.0–132.5 | 99.7 ± 19.9 |
| **% of Standard length** | | | | | | |
| Body depth | 11.0 | 10.6–13.4 | 11.9 ± 1.0 | 11.2 | 11.3–15.1 | 12.9 ± 1.1 |
| Head length | 18.2 | 18.2–22.6 | 21.0 ± 1.4 | 19.0 | 17.0–21.1 | 19.2 ± 1.2 |
| Head depth | 9.3 | 8.7–11.6 | 10.5 ± 1.0 | 11.2 | 9.6–12.6 | 11.0 ± 0.8 |
| Head width | 11.0 | 11.2–13.4 | 12.2 ± 0.7 | 12.2 | 11.2–13.4 | 12.2 ± 0.6 |
| Snout length | 8.4 | 8.0–10.0 | 9.1 ± 0.6 | 8.6 | 7.8–10.0 | 8.7 ± 0.6 |
| Eye diameter | 3.3 | 2.9–4.4 | 3.6 ± 0.5 | 2.7 | 2.1–3.1 | 2.6 ± 0.2 |
| Interorbital width | 4.9 | 3.9–6.1 | 5.1 ± 0.6 | 4.8 | 4.3–6.6 | 5.3 ± 0.7 |
| Dorsal-fin length | 10.7 | 9.1–13.6 | 11.4 ± 1.7 | 9.4 | 8.9–12.9 | 10.6 ± 1.4 |
| Pectoral-fin length | 10.9 | 9.2–15.6 | 13.6 ± 2.2 | 12.3 | 11.1–15.2 | 13.1 ± 1.3 |
| Pelvical-fin length | 10.0 | 8.2–13.0 | 11.3 ± 1.7 | 10.5 | 9.2–12.7 | 10.7 ± 1.0 |
| Anal-fin length | 10.8 | 9.5–12.7 | 10.9 ± 1.1 | 12.9 | 11.8–14.5 | 13.0 ± 0.7 |
| Vent to caudal-fin origin | 31.4 | 27.8–35.5 | 30.4 ± 2.4 | 32.1 | 30.0–35.4 | 32.6 ± 1.8 |
| Prepectoral length | 18.5 | 16.4–24.0 | 21.1 ± 2.3 | 17.2 | 16.2–19.6 | 17.8 ± 1.0 |
| Predorsal length | 43.7 | 42.3–49.3 | 46.7 ± 2.1 | 47.1 | 42.1–49.9 | 45.5 ± 1.8 |
| Prepelvic length | 45.7 | 44.7–52.4 | 48.6 ± 2.2 | 46.5 | 42.4–50.2 | 46.2 ± 2.4 |
| Preanal length | 70.9 | 70.5–75.2 | 73.0 ± 1.4 | 71.0 | 67.2–73.6 | 70.7 ± 1.7 |
| Caudal-peduncle length | 20.0 | 17.6–22.2 | 19.3 ± 1.5 | 21.0 | 17.9–22.9 | 20.5 ± 1.5 |
| Caudal-peduncle depth | 9.4 | 8.0–10.4 | 9.3 ± 1.0 | 9.7 | 9.0–11.0 | 10.0 ± 0.6 |
| Caudal-fin length | 12.3 | 11.8–15.9 | 14.6 ± 1.3 | 12.5 | 12.0–15.5 | 13.5 ± 1.2 |
| **% of Head length** | | | | | | |
| Head depth | 51.0 | 47.1–53.3 | 49.8 ± 2.8 | 59.2 | 54.0–60.8 | 57.5 ± 2.2 |
| Head width | 60.4 | 53.5–61.4 | 58.2 ± 2.5 | 64.0 | 60.6–68.0 | 63.8 ± 2.0 |
| Snout length | 46.3 | 40.5–45.5 | 43.5 ± 2.0 | 45.3 | 41.8–50.2 | 45.7 ± 2.5 |
| Eye diameter | 18.1 | 14.4–19.4 | 16.9 ± 1.9 | 14.1 | 11.8–15.1 | 13.7 ± 0.9 |
| Interorbital width | 26.8 | 21.4–27.8 | 24.4 ± 2.2 | 25.4 | 24.0–32.0 | 27.7 ± 2.2 |
| **% of Interorbital width** | | | | | | |
| Eye diameter | 67.8 | 58.2–78.0 | 68.4 ± 7.5 | 55.5 | 41.5–56.7 | 49.8 ± 4.2 |
| **% of caudal-peduncle length** | | | | | | |
| Caudal-peduncle depth | 47.0 | 42.0–53.8 | 47.3 ± 4.5 | 46.2 | 40.4–55.2 | 49.1 ± 4.9 |
| P | i, 10 | i, 9–11 | | i, 10 | i, 9–11 | |
| D | iii, 9 | iii, 9 | | iii, 9 | iii, 9 | |
| V | i, 7 | i, 7–8 | | i, 7 | i, 7–8 | |
| A | iii, 5 | iii, 5 | | iii, 5 | iii, 5 | |
| C | 9+8 | 9+8 | | 9+8 | 9+8 | |
| Vertebrae | 4+43 | 4+42–43 (n = 4) | | 4+42 | 4+42–43 (n = 4) | |

dorsolaterally in upper half of head, not reaching dorsal profile, when viewed laterally; eye diameter less than interorbital width. Anterior and posterior nostrils set closely; anterior nostril situated at end of small and oblique tube. Mouth inferior; lips thick, slightly folded, smooth with small median incision in upper lip and marked median longitudinal groove on lower lip. Upper jaw with shallow processus dentiformis; lower jaw spoon-like, without median notch. Two pairs of rostral barbels; inner barbels extending close to rictus and outer barbels reaching rictus. Maxillary barbels rooted in corners of mouth, extending close to vertical through middle of eye.

Cephalic lateralis system with 8 supraorbital, 4+10 infraorbital, 9 pre-operculo-mandibular and 3 supratemporal pores. Gill opening large, with its upper extremity aligned with centre of orbit.

Fin rays flexible. Dorsal fin with 3 unbranched and 9 branched rays; longest ray shorter than dorsal-fin base; distal margin slightly convex; origin closer to snout tip than to caudal-fin base. Pectoral fin with one unbranched and 9–11 branched rays, tip of depressed fin not reaching mid-way between pectoral- and pelvic-fin insertion. Pelvic fin with one unbranched and 7–8 branched rays, reaching about half the distance between pelvic-fin insertion and anus; origin of pelvic fin at vertical of 1st or 2nd branched dorsal fin ray. Axillary lobe present on pelvic-fin base. Anus set closer to anal-fin origin than to pelvic-fin insertion; separated from anal-fin origin by distance 1.2–1.5 times greater than eye diameter. Anal fin with 3 unbranched and 5 branched rays, tip of depressed fin not reaching caudal-fin base; distal margin slightly convex. Caudal fin with 9+8 branched rays and truncate with slightly concave outer margin.

Vertebrae 4+42–43 (n = 5), including 20–21 abdominal and 22 caudal vertebrae. Gas bladder bipartite; anterior chamber invisible, fully enclosed in capsule; posterior chamber degenerative. Intestine with a distinct transverse bend not reaching posterior end of U-shaped stomach.

**Colouration.** In formalin-stored specimens (Fig. 1), ground colour of body yellowish, with light yellowish ventral surface. Head yellowish with vermiform marks; snout, lips and anterior nostril light white. Thirteen to fourteen brown vertical bars on flank; anterior six or seven bars oval and closely set, but six post-dorsal bars nearly oblong and deep. Four or five brown rounded bars along dorsal mid-line of predorsal body; last three bars merged into a brown band in some individuals; some brown bars of irregular shape inserted between rounded bars along dorsal mid-line and vertical bars on flank, less or more touched with these bars and sometimes merged to form discontinuous brown band. Some irregular brown bars present on dorsum from behind dorsal-fin origin to anterior end of adipose crest amongst dorsal mid-line of caudal peduncle. A brown lateral stripe extending along base of dorsal adipose crest. Melanin pigments on branched rays forming proximal and subdistal brownish bands across dorsal fin. Pectoral, pelvic and anal fins translucent white yellowish. Caudal fin greyish with some dark black spots and blackish distal edge. Caudal-fin base with dark brown vertical bar. In freshly-collected individuals (Fig. 2), overall body colouration very similar to that of formalin-preserved specimens, but a little bright. Caudal fins and dorsal adipose crest red, particularly in spawning season.

**Distribution.** The type specimens were collected from Qingshui-He, tributary to Wu-Jiang of upper Chang-Jiang Basin in Guizhou Province, China. The species is also known from upstream of Mengjiang, tributary to Zhu-Jiang Basin in Huaxi District of Guiyang City and Changshun County of Qiannan Prefecture, Guizhou Province, China (Fig. 3).

**Etymology.** The specific epithet, used as a noun, is named after 'Xiangzhi'. This Chinese word means fragrant paper. The type locality (Xiangzhi-Gou) is named after the local intangible cultural heritage, the fragrant paper manufacturing technique. A corresponding common Chinese name "香纸荷马条鳅" is proposed here for the new species.

### *Homatula shexiang* Cao, Liu, Zeng & Zhang, sp. nov.

https://zoobank.org/398A7428-A3A6-450B-96A7-76818EE2E333

Figs 4, 5

*Nemachelius variegatus*: Wu, 1987: 27 (Wu-Jiang).

*Paracobitis variegatus*: Ding, 1994: 51 (Wu-Jiang).

**Holotype.** IHB 202006048998, 100.2 mm SL; China: Guizhou: Guiyang City: Xiuwen District: Maodong-He, a stream tributary to Maotiao-He, under Wugong Bridge (26°54'11"N,106°29'22"E); collected by D. M. Guo and W. H. Shao, June 2020.

**Paratypes.** IHB202006048993–8997, 202006048999–9002, 202006200601–0602, 11 specimens, 71.9–125.6 mm SL; other date same as holotype. IHB 202006048907–8911, five specimens, 71.0–132.5 mm SL; China: Guizhou: Guiyang City: Kaiyang District: Macha-He (27°7'14"N, 107°0'1"E), a stream tributary to Qingshui-He; collected by D. M. Guo and W. H. Shao, June 2020.

**Diagnosis.** A member of the partially scaled group of *Homatula* defined by having a sparsely scaled or unscaled predorsal body. It differs from all other eight species of this group, except *H. longidorsalis* in possessing 9 (vs. 7 or 8) branched dorsal-fin rays. *Homatula shexiang* differs from this species in having an adipose crest along the dorsal mid-line of the caudal peduncle anteriorly terminating vertically away from the anal-fin origin (vs. above the anal-fin origin), a deep (vs. shallow) head (depth 54.0–60.8% of its length vs. 46.46–48.65%) and a slender (vs. stout) caudal peduncle with (depth 40.4–55.2% vs. 57.2–61.5% of its length).

**Description.** Morphometric measurements for type specimens given in Table 2. General appearance of holotype shown in in Fig. 4.

Body elongated, anteriorly cylindrical and posteriorly compressed laterally, with uniform depth from behind head to caudal-fin base. Ventral profile of head straight or slightly concave; ventral profile of head and body almost straight or slightly concave from pectoral-fin insertion to anal-fin origin and slightly convex from anal-fin origin to caudal-fin base. Body partially scaled; no scales on predorsal body, but scales only present on body behind dorsal-fin origin. Lateral line complete, with 85–95 pored scales, extending along mid-lateral body to caudal-fin base. Adipose crests along dorsal and ventral mid-lines of caudal peduncle supported by rudimentary rays. Dorsal adipose crest anteriorly terminating beyond the posterior end of the anal-fin base, but away from anal-fin origin.

Head relatively long and slightly depressed, wider than deep. Snout blunt in lateral view, slightly shorter

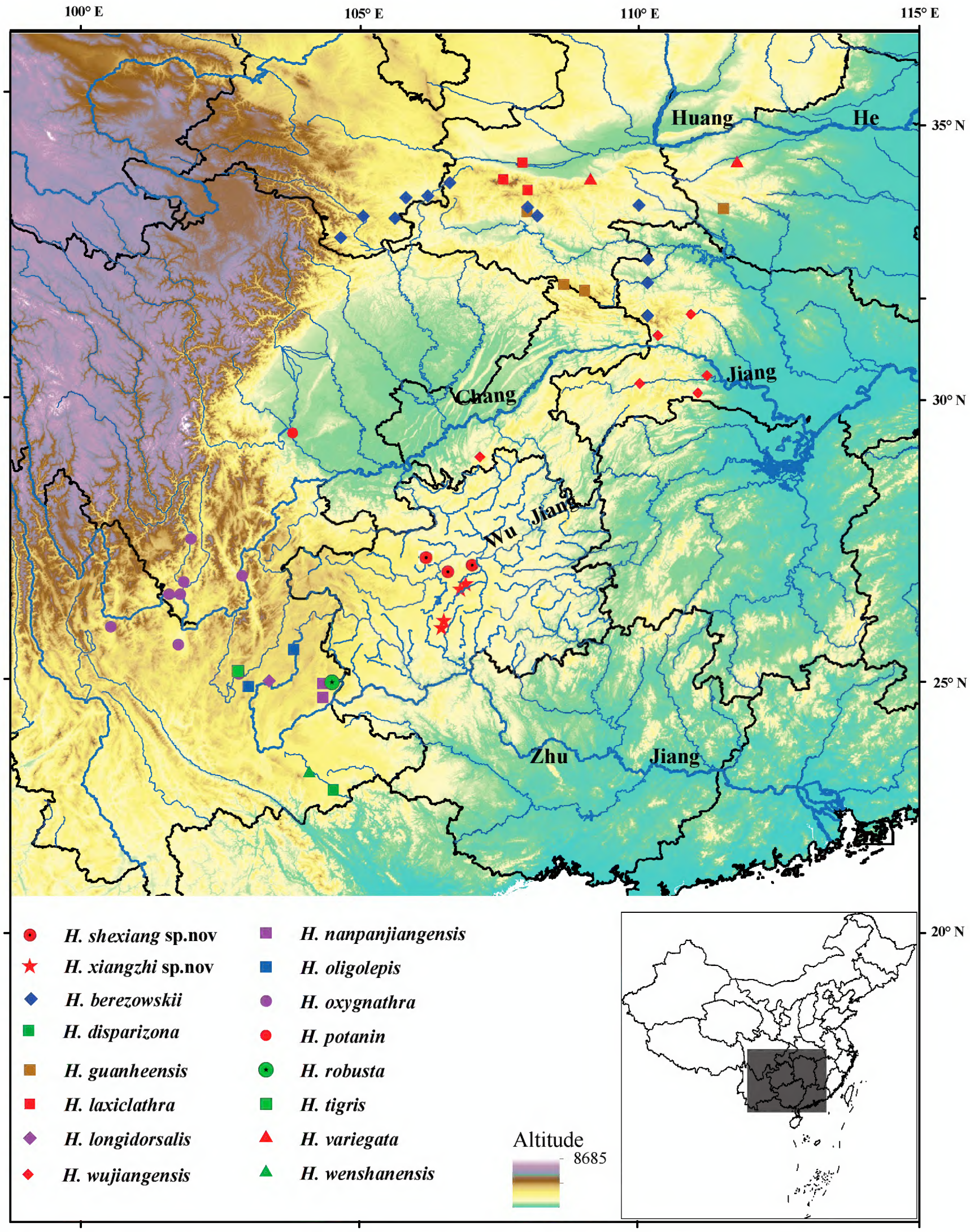


**Figure 3.** Distribution of the partially scaled and the scaleless group of *Homatula* in China.

than postorbital head. Eye oval with slightly convex interorbital space, positioned dorsolaterally in upper half of head, not reaching dorsal profile when viewed laterally; diameter less than interorbital width. Anterior and posterior nostrils set closely; anterior nostril situated at end of small and oblique tube. Mouth inferior; lips slightly thick, slightly folded and smooth with small median incision in upper lip and marked median longitudinal groove on lower lip. Upper jaw with shallow processus dentiformis and lower jaw spoon-like without median notch. Two pairs of rostral barbels; inner barbels extending to rictus and outer barbels reaching rictus. Maxillary barbels rooted in corners of mouth, extending close to vertical through middle of eye, but short of posterior margin of eye. Cephalic lateralis system with 8 supraorbital, 4+10 infraorbital, 9 preoperculo-mandibular and 3 supratemporal pores. Gill opening large, with its upper extremity aligned with centre of orbit.

Fin rays flexible. Dorsal fin with 3 unbranched and 9 branched rays; longest ray shorter than dorsal-fin base;

**Table 3.** Genetic distances of Cyt b amongst species of *Homatula*.

| Species | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***H. shexiang* sp.nov.** | 1 | | | | | | | | | | | | | | | | | | | | | | | | |
| ***H. xiangzhi* sp.nov.** | 2 | 3.6 | | | | | | | | | | | | | | | | | | | | | | | |
| *H. tigris* | 3 | 6.7 | 7.9 | | | | | | | | | | | | | | | | | | | | | | |
| *H. variegata* | 4 | 7.8 | 7.8 | 8.5 | | | | | | | | | | | | | | | | | | | | | |
| *H. berezowskii* | 5 | 7.7 | 8.0 | 8.0 | 3.2 | | | | | | | | | | | | | | | | | | | | |
| *H. guanhensis* | 6 | 7.6 | 7.7 | 8.4 | 1.4 | 3.0 | | | | | | | | | | | | | | | | | | | |
| *H. laxiclathra* | 7 | 6.8 | 7.3 | 8.0 | 4.8 | 4.6 | 4.6 | | | | | | | | | | | | | | | | | | |
| *H. oxygnathra* | 8 | 7.8 | 7.7 | 8.1 | 5.3 | 4.9 | 5.1 | 2.1 | | | | | | | | | | | | | | | | | |
| *H. longidorsalis* | 9 | 6.7 | 7.2 | 7.4 | 5.7 | 5.5 | 5.7 | 4.7 | 5.1 | | | | | | | | | | | | | | | | |
| *H. nanpanjiangensis* | 10 | 7.4 | 7.1 | 6.7 | 5.1 | 5.1 | 5.2 | 4.4 | 4.8 | 4.5 | | | | | | | | | | | | | | | |
| *H. wujiangensis* | 11 | 8.5 | 8.9 | 10.0 | 9.3 | 8.9 | 9.3 | 8.9 | 9.3 | 8.7 | 8.2 | | | | | | | | | | | | | | |
| *H. potanini* | 12 | 8.6 | 8.4 | 10.2 | 8.8 | 8.8 | 8.7 | 8.8 | 9.2 | 8.6 | 8.1 | 1.1 | | | | | | | | | | | | | |
| *H. anguillioides* | 13 | 8.2 | 8.7 | 8.2 | 9.7 | 9.4 | 9.5 | 9.1 | 9.3 | 8.4 | 7.8 | 9.7 | 9.5 | | | | | | | | | | | | |
| *H. acuticephala* | 14 | 8.4 | 8.6 | 8.3 | 9.6 | 9.3 | 9.4 | 9.0 | 9.2 | 8.3 | 7.7 | 9.5 | 9.4 | 0.1 | | | | | | | | | | | |
| *H. anteridorsalis* | 15 | 10.3 | 10.1 | 10.8 | 11.0 | 11.1 | 10.6 | 10.5 | 10.4 | 9.9 | 9.1 | 11.2 | 10.9 | 4.1 | 4.0 | | | | | | | | | | |
| *H. cryptoclathrata* | 16 | 9.8 | 9.8 | 10.4 | 10.6 | 10.5 | 10.1 | 9.7 | 9.7 | 9.5 | 8.8 | 10.6 | 10.5 | 3.8 | 3.7 | 1.8 | | | | | | | | | |
| *H. disparizona* | 17 | 8.1 | 8.6 | 9.0 | 9.8 | 9.4 | 10.0 | 8.4 | 8.8 | 8.2 | 7.5 | 9.7 | 9.8 | 8.5 | 8.6 | 10.0 | 9.3 | | | | | | | | |
| *H. geminusclathrata* | 18 | 12.5 | 11.5 | 12.9 | 14.8 | 14.2 | 14.5 | 14.6 | 14.4 | 13.0 | 13.0 | 13.2 | 13.0 | 11.9 | 12.0 | 13.0 | 12.9 | 13.2 | | | | | | | |
| *H. longibarbata* | 19 | 8.8 | 8.3 | 9.6 | 10.5 | 9.9 | 10.1 | 9.5 | 9.2 | 9.2 | 8.3 | 9.3 | 9.1 | 4.2 | 4.1 | 4.2 | 4.3 | 9.8 | 11.6 | | | | | | |
| *H. microcephala* | 20 | 10.2 | 10.3 | 10.0 | 11.0 | 10.8 | 11.1 | 11.0 | 10.9 | 9.8 | 9.6 | 10.3 | 10.3 | 4.5 | 4.5 | 4.2 | 4.1 | 9.5 | 11.6 | 4.9 | | | | | |
| *H. nigra* | 21 | 9.8 | 10.0 | 10.1 | 10.4 | 10.4 | 10.3 | 9.8 | 9.6 | 9.2 | 8.9 | 10.5 | 10.2 | 4.2 | 4.2 | 2.4 | 1.5 | 8.8 | 11.6 | 4.0 | 2.7 | | | | |
| *H. pycnolepis* | 22 | 9.0 | 9.8 | 8.8 | 10.5 | 10.1 | 10.2 | 9.5 | 9.9 | 8.9 | 8.4 | 9.8 | 9.8 | 3.3 | 3.4 | 4.0 | 3.9 | 8.6 | 11.4 | 4.1 | 4.5 | 3.7 | | | |
| *H. wuliangensis* | 23 | 12.0 | 11.0 | 12.5 | 14.3 | 13.7 | 14.1 | 14.0 | 13.8 | 12.7 | 12.5 | 12.8 | 12.5 | 11.6 | 11.7 | 12.9 | 12.6 | 12.6 | 0.5 | 11.4 | 11.4 | 11.4 | 11.2 | | |
| *H. wenshanensis* | 24 | 8.1 | 8.2 | 9.2 | 9.9 | 9.7 | 10.0 | 8.4 | 8.4 | 8.0 | 7.5 | 9.2 | 9.3 | 9.0 | 9.1 | 10.4 | 9.9 | 3.7 | 13.0 | 9.0 | 9.9 | 9.6 | 8.5 | 12.5 | |
| *H. dotui* | 25 | 14.1 | 14.7 | 14.7 | 14.8 | 14.2 | 14.7 | 14.3 | 13.5 | 13.0 | 13.1 | 13.3 | 13.3 | 13.8 | 13.7 | 14.6 | 15.2 | 13.7 | 16.6 | 13.4 | 14.7 | 15.0 | 13.9 | 16.0 | 12.9 |

**Figure 4.** *Homatula shexiang* sp. nov., IHB 202006048998, holotype, 100.2 mm SL; China: Guizhou: Guiyang City: Xiuwen District: Maodong-He, a stream tributary to Maotiao-He, under Wugong Bridge. Lateral (upper), dorsal (middle) and ventral (lower) view.

**Figure 5.** Freshly-captured individual of *Homatula shexiang* sp.nov. collected from China: Guizhou: Qianxi City:Wei-he.

distal margin slightly convex. Pectoral fin with one unbranched and 9–11 branched rays, tip of depressed fin not reaching mid-way between pectoral- and pelvic-fin insertion. Pelvic fin with one unbranched and 7–8 branched rays, reaching about mid-way between pelvic-fin insertion and anus; origin of pelvic fin at vertical of 1st or 2nd branched dorsal fin ray. Anus positioned closer to anal-fin origin than to pelvic-fin insertion; separated from anal-fin origin by distance 1.5–2 times greater than eye diameter. Anal fin with 3 unbranched and 5 branched rays, tip of depressed fin not reaching caudal-fin base; distal margin slightly convex. Caudal fin rounded; upper and lower lobes with 9 and 8 branched rays, respectively.

Vertebrae 4+42–43 (n = 4), including 20–21 abdominal and 22 caudal vertebrae. Gas bladder bipartite; anterior chamber invisible, fully enclosed in capsule; posterior chamber degenerative. Intestine with a distinct transverse bend not reaching posterior end of U-shaped stomach.

**Colouration.** In formalin-stored specimens (Fig. 4), ground colour of body yellowish. Dorsal and lateral head yellowish with vermiform brown marks; ventral head yellow, with white snout, lips and barbels. Eight or nine brown irregularly-shaped bars along dorsal mid-line of body from behind head to origin of dorsal adipose crest. Thirteen to fifteen brown vertical bars on flank; anterior nine bars usually confused with brown bars along dorsal mid-line of body and wider than interspace space; three or four brown vertical bars on caudal peduncle equal to interspace width. Ventral body surface white-yellow. Melanin pigments on branched rays to form proximal and subdistal brownish bands across dorsal fin. Pectoral, pelvic fins and anal fin translucent white-yellow. Caudal fin and adipose crest dusky, sometimes with some blackish spots. Caudal-fin base with a dark brown vertical bar. In freshly-collected specimens (Fig. 5), overall body colouration similar to that in formalin-stored specimens, but a little bright. Caudal fin and dorsal adipose crest reddish, particularly during spawning season.

**Distribution.** To date, known only from Wu-Jiang, tributary to upper Chang-Jiang in Guiyang and Qianxi, Guizhou Province, China (Fig. 3).

**Etymology.** The specific epithet, here used as a noun, is named after Mrs. She Xiang (奢香夫人), an outstanding female politician and the leader of the Yi nationality in Guizhou Province during the Min Dynasty. The Wugong Bridge, type locality of the new species, is one of stone bridges across the Maodong-He built by Mrs. She Xiang six hundred years ago. A corresponding common name "奢香荷马条鳅" in Chinese is proposed here for this new species.

## Phylogenetic analysis and genetic distances

A total of 16 Cytb gene sequences with 1080 bp in length were amplified in this study. The molecular phylogenetic trees generated from the BI and ML analyses showed the same topologies, only the BI tree with Bayesian posterior probabilities (PP) and bootstrap support (BS) value being presented in Fig. 6. From the tree topologies, species of *Homatula* in China form a monophyletic clade with a high support. The two new species, *H. shexiang* sp. nov. and *H. xiangzhi* sp. nov., formed a highly-supported lineage itself and then constituted a well-supported clade which was sister to the species *H. tigris* with weak support. This group consisting of the three species was recovered as the sister to a well-supported clade formed by seven other species distributed in the Chang-Jiang, Huang-He and Nanpan-Jiang drainage areas.

The genetic distances between the *Homatula* species are provided in Table 3. Interspecific genetic distance between the two new species, *H. shexiang* and *H. xiangzhi* and other congeneric species ranged from 6.7% to 12.5% and 7.1% to 11.5% (Table 4), respectively. Interspecific genetic distance between the two new species was 3.6% and intraspecific genetic divergence was 0.61% and 0.06% for *H. shexiang* and *H. xiangzhi*, respectively. The molecular phylogenetic results supported *H. shexiang* and *H. xiangzhi* to be two distinct species.

# Discussion

Body squamation is of taxonomic importance in species recognition of *Homatula*. All currently-recognised species of this genus can be divided into three groups: the scaled, the partially scaled and the scaleless (Li et al. 2019). *Homatula shexiang* and *H. xiangzhi* are respectively assigned

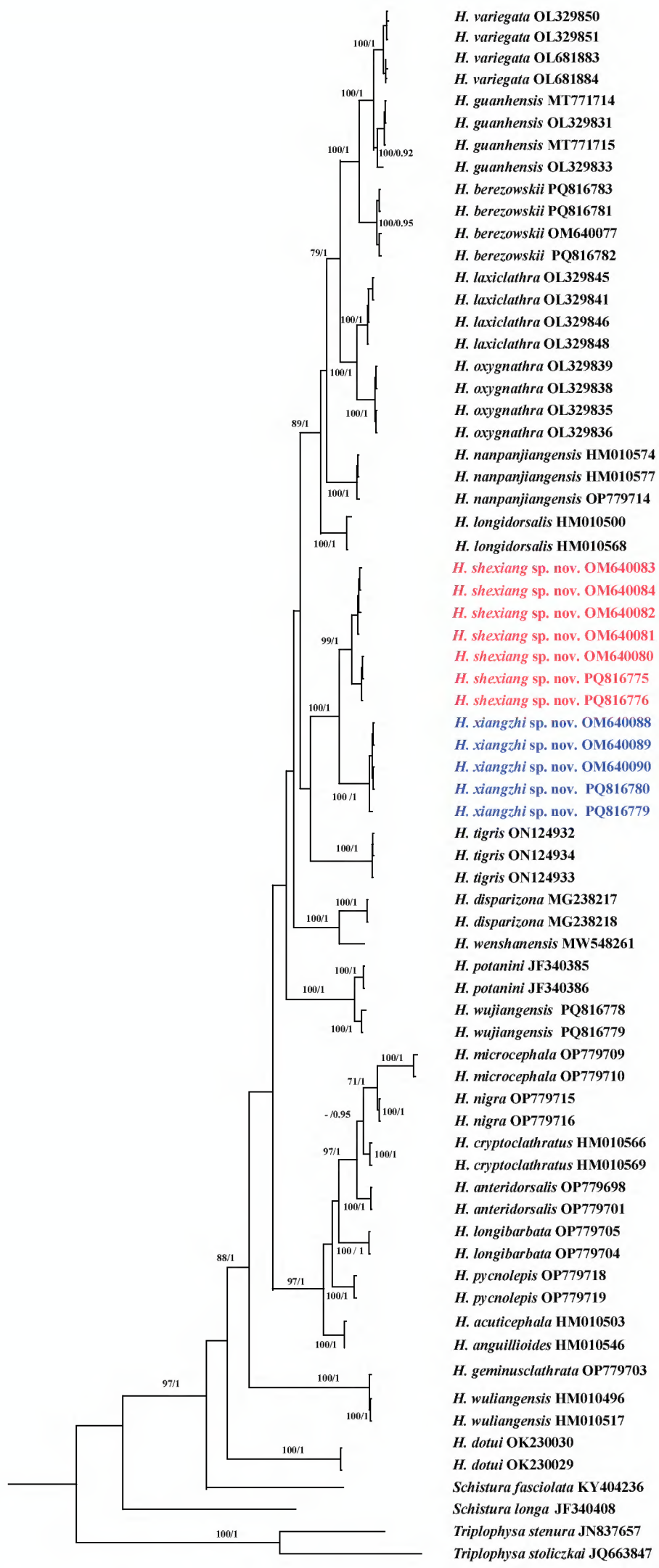


**Figure 6.** Bayesian Inference tree generated from the Cytb gene from species of *Homatula*. Nodal numbers indicate Bayesian posterior probabilities (> 0.9) and Maximum Likelihood bootstrap values (> 70%), respectively.

to the partially scaled group and the scaleless group. Each of both has remarkable morphological differences with all other members of the species group to which it is designated (Table 4). See the diagnosis and Table 4 for morphological variations between *H. xiangzhi* and other six species of the scaleless group, including *H. disparizona*, *H. nanpanjiangensis*, *H. oligolepis*, *H. robusta*, *H. wenshanensis* and *H. wujiangensis*. In the original description by Nguyen et al. (2021), *H. dotui* was referred to the scaleless group of this genus. Molecular analysis showed that *H. dotui* was distantly related to sampled Chinese congeneric species, indicating that it is not a member of this genus (Li et al. 2022). For this reason, this species is removed from *Homatula* in this study and its generic classification needs in-depth research. Likely, it belongs to its own genus.

*Homatula shexiang* has a sparsely scaled predorsal body, with its postdorsal portion fully covered with scales. It is thus assigned to the partially-scaled group of *Homatula*. Other eight congeneric species currently referred to this group are *H. berezowskii*, *H. guanheensis*, *H. laxiclathra*, *H. longidorsalis*, *H. oxygnathra*, *H. potanini*, *H. tigris* and *H. variegata*. Major diagnostic characters amongst these partially-scaled species are summarised in Table 4. *Homatula shexiang* has marked morphological variations with *H. longidorsalis* (see the diagnosis of this new species). Nine branched dorsal-fin rays can distinguish both from all other members of the partially-scaled group, with seven or eight rays. *Homatula shexiang* is further separated from these species by possessing a complete lateral line (vs. incomplete in *H. potanini*), an elongate (vs. robust) body with a uniform (vs. non-uniform, slightly declining towards the caudal-fin base in *H. potanini*) depth, no median notch on the lower jaw (vs. present in *H. variegata*, *H. berezowskii*, *H. guanheensis*, *H. laxiclathra* and *H. potanini*), a longer (vs. shorter) snout (length 41.8–50.2%, mean 45.7% of HL vs. 37.0–41.7% in *H. potanini* and 22.7–30.7%, mean 27.6% in *H. tigris*), a gill opening with the upper extremity aligning with the centre of orbit (vs. the lower edge of orbit in *H. berezowskii*, *H. guanheensis* and *H. oxygnathra*), pelvic-fin origin inserted vertically behind (vs. opposite in *H. variegata* and *H. laxiclathra*) dorsal fin origin, an adipose crest along the dorsal mid-line of the caudal peduncle anteriorly terminating beyond the posterior end of the anal-fin base, but beyond anal-fin origin (vs. above or beyond the anal-fin origin in *H. oxygnathra*, *H. potanini* and *H. tigris* or above the posterior end of the anal-fin base in *H. variegata*, *H. berezowskii*, *H. guanheensis* and *H. laxiclathra*) (see Table 4).

The validity of the two new species is each corroborated by its monophyletic nature recovered in the Cytb gene-based phylogenetic analysis (Fig. 6) and its distinct genetic divergence with all other sampled congeneric species (Table 3). Both were previously misidentified as *H. variegata* from the Wu-Jiang of the upper Chang-Jiang Basin (Wu 1989; Ding and Deng 1990). In the BI and ML trees, based on the Cytb gene (Fig. 6), both were sister to each other, but distantly allied to *H. variegata* s. str. from the Wei-He of the Huang-He Basin. Each of the two new species had an interspecific genetic distance of 6.7% to 12.5% and 7.1% to 11.5% with all other sampled congeneric species, respectively (Table 3). Their interspecific sequences divergence was 3.6%, greater than the threshold value 2%

**Table 4.** Major diagnostic characters for the partially scaled group and the scaleless group of *Homatula* in China.

| Species | Characters | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Body squamation | Caudal-peduncle depth (% of its length) | Median notch on lower jaw | Pelvic-fin origin | Dorsal fin branched rays | Anterior end of dorsal adipose crest of caudal peduncle | Caudal-fin shape | Lateral line | Vertebrae |
| *H. variegata* | Postdorsal body scaled, predorsal body scales sparse | 36.4–46.6 | Present | Opposite to dorsal fin insertion | 8 | Above the posterior end of the anal-fin base | Broadly rounded | Complete | 4+42–44 |
| *H. laxiclathra* | | 38.9–57.1 | Present | Opposite to dorsal fin insertion | 8 | Above the posterior end of the anal-fin base | Obliquely truncate | Complete | 4+43–44 |
| *H. berezowskii* | | 33.9–63.4 | Present | At vertical of 1st or 2nd branched dorsal fin ray | 8 | Above the posterior end of the anal-fin base | Truncate | Complete | 4+42–44 |
| *H. guanheensis* | | 46.1–65.0 | Present | Opposite to dorsal fin insertion | 7–8 | Above the posterior end of the anal-fin base | Truncate | Complete | 4+41–43 |
| *H. oxygnathra* | | 45.1–56.0 | Absent | At vertical of 1st or 2nd branched dorsal fin ray | 8 | Above the anal fin origin | Obliquely truncate | Complete | 4+42–44 |
| *H. longidorsalis*[a] | | 57.2–61.5 | Absent | At vertical of 1st or 2nd branched dorsal fin ray | 9 | Above the anal fin origin | Obliquely truncate | Complete | 4+42–44 |
| *H. potanini*[b] | | 95.0–136.4 | Present | At vertical of 1st or 2nd branched dorsal fin ray | 8 | Above the anal fin origin | Rounded or truncate | Incomplete | 4+35–36 |
| *H. tigris*[c] | | 43.1–55.3 | Absent | At vertical of 1st or 2nd branched dorsal fin ray | 8 | Beyond anal-fin origin | slightly emarginate | Complete | 4+40–41 |
| ***H. shexiang* sp.nov.** | | 42.0–53.8 | Absent | At vertical of 1st or 2nd branched dorsal fin ray | 9 | Vertically away from the anal-fin origin but beyond the posterior end of the anal-fin base | Obliquely truncate | Complete | 4+42–43 |
| ***H. xiangzhi* sp.nov.** | Body scaleless or only a few scales covering the caudal peduncle | 42.0–57.8 | Absent | At vertical of 1st or 2nd branched dorsal fin ray | 9 | Vertically away from the anal-fin origin, but beyond the posterior end of the anal-fin base | Obliquely truncate | Complete | 4+42–43 |
| *H. oligolepis*[d] | | 51.0–57.0 | Present | At vertical of 1st or 2nd branched dorsal fin ray | 9 | Above the anal fin origin | Broadly rounded | Complete | 4+39–41 |
| *H. nanpanjiangensis*[d] | | 50.0–70.0 | Present | At vertical of 1st or 2nd branched dorsal fin ray | 8–9 | Above the anal fin origin | Emarginated | Complete | 4+36–38 |
| *H. disparizona*[e] | | 47–62 | Absent | Opposite to dorsal fin insertion | 7–8 | Beyond anal-fin origin | Emarginate | Complete | 4+39–40 |
| *H. robusta*[f] | | 70.5–78.5 | Present | At vertical of 1st or 2nd branched dorsal fin ray | 8 | Beyond anal-fin origin | Emarginated | Complete | 4+37–39 |
| *H. wujiangensis*[b] | | 100–120 | Present | At vertical of 1st or 2nd branched dorsal fin ray | 8 | Vertically away from the anal-fin origin but beyond the posterior end of the anal-fin base | Truncate | Incomplete | 4+35–36 |
| *H. wenshanensis*[g] | | 27.3–35. 0 | Present | At vertical of 1st or 2nd branched dorsal fin ray | 7 | Above the posterior end of the anal-fin base | Furcate | Complete | 4+47–48 |

a: morphometric measurements data used here is from Min and Yang (2021); b: morphometric measurements data used here is from Guo et al. (2021); c: the data used here is from Che et al. (2023); d: the data used here is from Min et al. (2010); e: the data used here is from Min et al. (2013); f: the data used here is from Min et al. (2022); g: the data used here is from Yang et al. (2017).

(Avise and Walker 1999) and the minimum value here detected between *H. variegata* and *H. guanheensis* (1.4%).

There are distinctive morphological differences between the two new species. Both differ from each other in head depth (47.1–53.3%, mean 49.8% of HL, vs. 54.0–60.8%, mean 57.5; see Fig. 7A); and eye size (diameter 58.2–78.0%, mean 68.4% of the interorbital width vs. 41.5–56.7%, mean 49.8%, see Fig. 7B) (Table 2). They also differ in body squamation; *H. shexiang* possesses a scaled post-dorsal body, but a scaleless body is found in *H. xiangzhi*. In addition, *H. xiangzhi*, based on Micro-CT scanned imagines, develops an inverted T-shaped supra-ethmoid-ethmoid complex with a vertical plate anteriorly bearing a more pronounced concavity when viewed laterally (Fig. 8). This contrasts with *H. shexiang* (5 specimens) that has a weakly-developed concavity

## Comparative material examined

***H. berezowskii.*** China: Gansu Province: Jialing-Jiang of upper Chang-Jiang Basin in Hui County, IHB 82V2385–2386, two topotypes, 116.5–86.9 mm SL; in Feng County, IHB 82VI2418, 82V2290–2293, 73VI1044–1045, seven specimens, 58.2–122.5 mm SL; in Wen County, IHB 64VI0135–0139, 64VI0601–0603, 78V0484–0485, ten specimens, 74.6–128.0 mm SL; in Wudu County, IHB 92VI2749–2757, nine specimens, 97.9–129.7 mm SL; in Kang County, IHB 82VI2489, one specimen, 126.1 mm SL; and in Cheng County, IHB 82VI2547–2550, four specimens, 72.4–88.4 mm SL. China: Shaanxi Province, Jialing-Jiang of upper Chang-Jiang Basin in

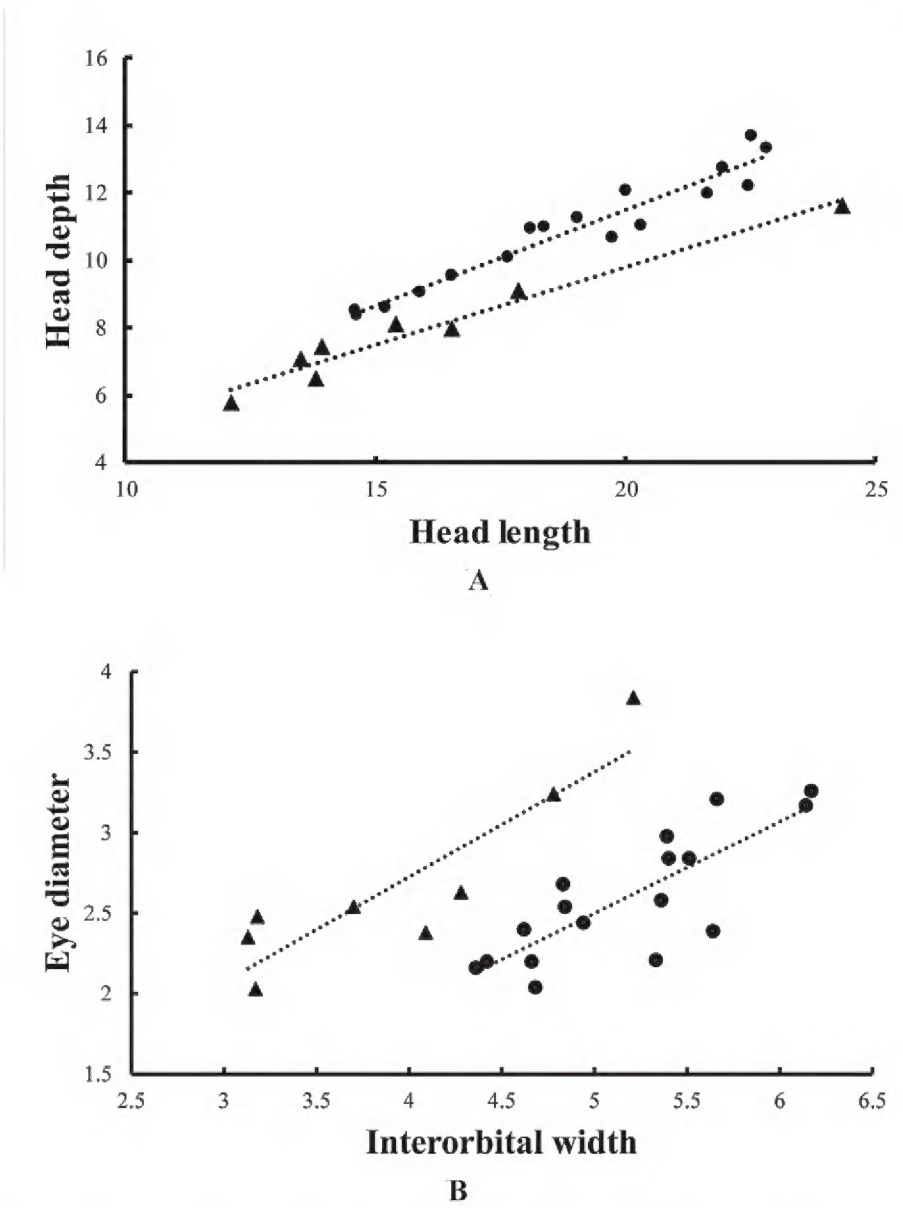


**Figure 7.** Comparisons of morphometric characters for two new species described in this study: *H. xiangzhi* sp.nov. (black triangle) and *H. shexiang* sp. nov. (black dot). **A.** Between head depth and its length (HL); **B.** Between eye diameter and interorbital width.

Fuoping County, IHB 80VI0869–0870, 80VI0874, 80VI0876–0881, nine specimens, 96.9–155.9 mm SL; in Ningshan County, IHB 80VI1032, one specimen, 89.7 mm SL; in Shanyang County, IHB 80VII1403, one specimen, 100.5 mm SL; in Jieyang County, IHB 73VI1191, 73VI1194, two specimens, 90.9–125.7 mm SL; in Baishu-Jiang, IHB 73VI1075, one specimen, 67.3 mm SL; and in Zhenba County, IHB 80VI1237–1241, 80VI1173–1174, 80VI1185, 80VI1176–1177, 80VI1181–1182, twelve specimens, 50.9–120.6 mm SL.

***H. disparizona.*** China: Yunnan Province: Red-He Basin, in Wenshan County, KIZ 2012000623, holotype, 76.0 mm SL (photograph examination). Data used in this study are from Min et al. (2013).

***H. guanheensis.*** China: Shaanxi Province: Han-Jiang of middle Chang-Jiang Basin, in Fuoping County: IHB 202106049918–9921, 202106055625–5627, seven specimens, 65.7–95.0 mm SL; in Langao County: IHB 202106049922–9923, 202106055640–5642, five specimens, 72.4 –135.9 mm SL.

***H. laxiclathra.*** China: Shaanxi Province: Wei-He of middle Huang-He Basin in Zhouzhi County, IHB 73V10738, 80VI0957, 82VI0103, 82VI0106–0108, 80VI0965–0968, 80VI0972, 11 type specimen, and IHB 202106049909–9912, 202106055611–5619, eight topotypes, 74.7–136.6 mm SL; in Taibai County, IHB 202106049899–9908, 10 specimens, 75.5–136.6 mm SL; and in Mei County, IHB 202106049888–9893, 202106049898, seven specimens, 65.6–131.3 mm SL.

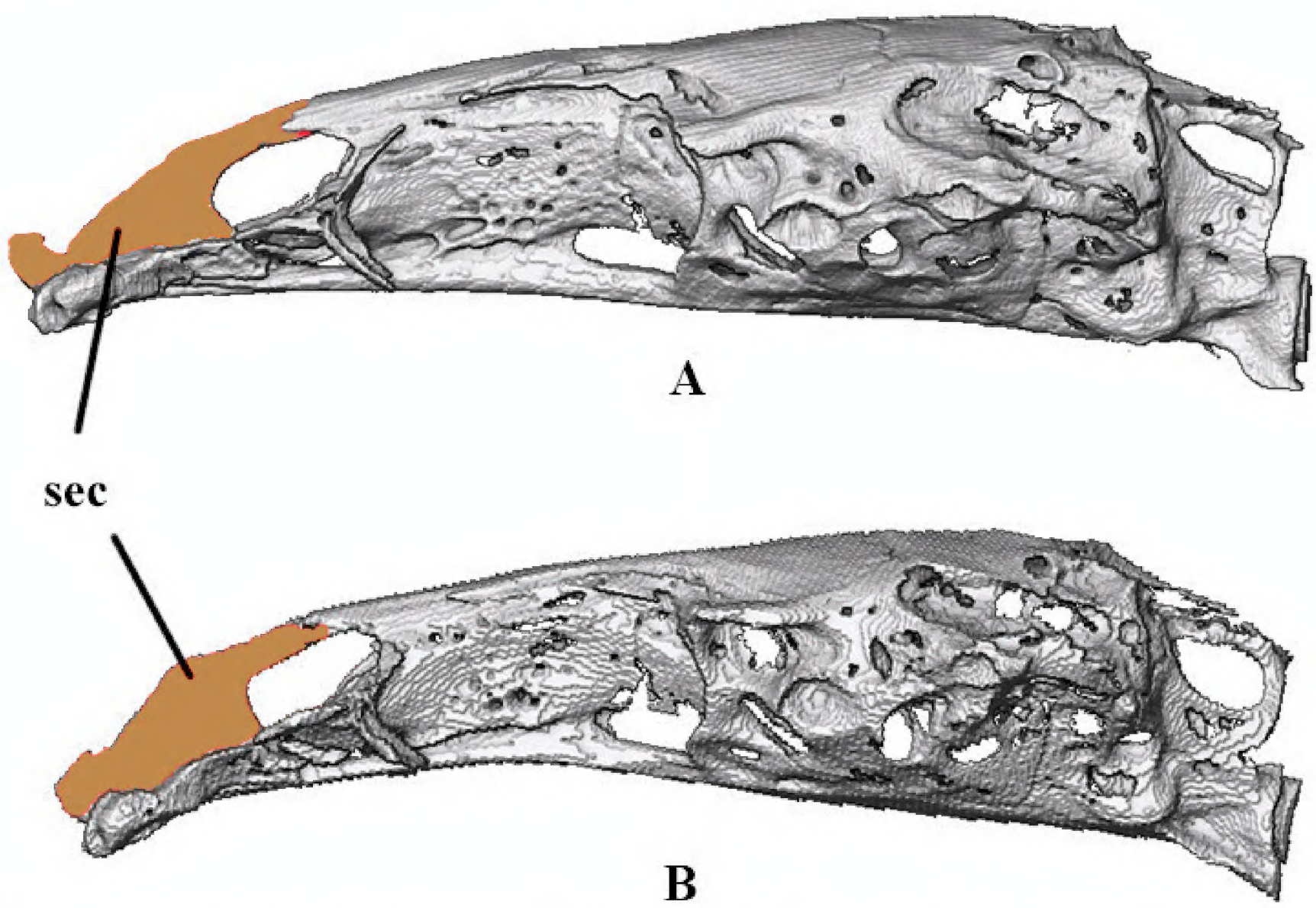


**Figure 8.** Lateral view of cranium of two new species described in this study. **A.** *H. xiangzhi* sp.nov. and **B.** *H. shexiang* sp.nov. sec: supraethmoid-ethmoid complex.

***H. longidorsalis.*** China: Yunnan Province: Nanpan-Jiang of Zhu-Jiang Basin in Yiliang County, KIZ 1987003989, holotype, 82.0 mm SL (photograph examination). China: Yunnan Province: Nanpan-Jiang of Zhu-Jiang Basin in Yiliang County, IHB 820093, one specimen, 155.9 mm SL. Morphometric measurements data used in this study are from Min and Yang (2021)

***H. nanpanjiangensis.*** China: Yunnan Province: Nanpan-Jiang of Zhu-Jiang Basin in Luoping County, KIZ 1994000023, holotype, 86.4 mm SL (photograph examination). Data from Min et al. (2010).

***H. oligolepis.*** China: Yunnan Province: Yangzong-Hai (= Lake) of Lancang-Jiang: IHB uncat, two type specimens, not in good condition. Morphometric measurements data from Zhu (1989) and Min et al. (2010).

***H. oxygnathra.*** China: Yunnan Province: upper Chang-Jiang Basin in Yuanmou County, BMNH-1908.2.27.23–24, lectotype and paralectotype, 86.7–113.3 mm SL, in Yunnan Fu (= Kunming City) (photograph examination); IHB 201909035461–5470, 10 specimens, 86.7–122.4 mm SL. China: Sichuan Province: upper Chang-Jiang Basin in Yanbian County, IHB 201909035805–5819, 15 specimens, 72.0–129.6 mm SL.

***H. potanini.*** China: Sichuan Province: Qingyi-Jiang of Chang-Jiang Basin in Emei City, IHB 42IX0661–2, 42IX0664, 42IX0666–7, 79IV0597–8, 79IV0600, 79IV0605, 79IV0609–10, 82V0301–4, 15 specimens, 68.6–83.3 mm SL. Morphometric measurements data used in this study are from Guo et al. (2021).

***H. variegata.*** China: Shaanxi Province: Wei-He of Huang-He Basin in Yenkiatsoun (= Baoji City), MNHN-IC-0000-7854, lectotype, and MNHN-B-2641, paralectotype, 96.8–103.5 mm SL; in Xi'an City, IHB 202106049914–9917, 202106055611–5614, topotypes, eight specimens, 65.9–122.4 mm SL.

***H. wujiangensis.*** China: Chongqing Province: Wu-Jinag of Chang-Jiang Basin in Jinfo Mountain, IHB 2017053707–3710, topotypes, four specimens, 40.5–76.3 mm SL.

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